ECOTONAL DISTRIBUTION OF SALT-TOLERANT SHRUBS IN THE NORTHERN MOJAVE DESERT

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ABSTRACT.— Ecotonal distribution of salt-tolerant shrubs was investigated under different kinds of edaphic conditions common to open and closed drainage basins in the northern Mojave Desert. Contributing causal factors involved changes in soil salinity, texture, and moisture stress. Varying degrees of halophytism occurred, ranging from plant species that are facultative in their adaptation to salinity to those that require comparatively high salt concentrations in soil for normal growth and development.

The main thrust of recent research on salt sensitivity has centered around osmotic and toxic effects of salts and the interaction between the various salts and ions adversely affecting plants (Strogonov 1962, Boyko 1966, Ranwell 1972, Waisel 1972, Reimold and Queen 1974, Poljakoff-Mayber and Gale 1975). Biological adaptation of the halophytes to salinity has occurred in different ways. Some halophytes absorb comparatively small amounts of salts as the result of unique biological properties. Others accumulate considerable amounts of salts in different plant parts that aid in the regulation of internal osmotic pressure. Some halophytes are capable of regulating their salt balance by mechanisms such as excretion of excess salts through special glands or abscission of leaves containing high levels of salt. Due to special biological features, halophytes can overcome the high osmotic pressure of the soil solution by decreasing their own osmotic potential. In such cases, rates of photosynthesis and transpiration are little influenced by high salt levels (Kleinkopf and Wallace 1974, Gale 1975). In certain plants this osmotic potential develops mainly from an accumulation of organic substances (Wallace and Kleinkopf 1974). In others it develops due to mineral salts absorbed from the saline soil substrate.

Environmental studies conducted in conjunction with nuclear weapons testing programs at the Nevada Test Site provided an opportunity to investigate some ecological characteristics of salt-tolerant shrubs in both open and closed drainage basins in the northern Mojave Desert (Wallace and Romney 1972, Romney et al. 1973, Wallace et al. 1973a, 1973b, 1974, Kleinkopf et al. 1975). The bajadas draining into playas of open and closed basins in southern Nevada often have prominent ecotonal demarcation lines below which certain plant species do not grow. Various hypotheses have been presented to explain ecotonal transition zones, including the influence of such factors as low temperature (Beatley 1974), salinity (Shreve 1940, Shantz and Piemeisel 1940), fine-textured soil (Gardner 1951, Branson et al. 1967), and excess of water (Fosberg 1940, Shreve and Wiggins 1964). These environmental factors were monitored as part of our environmental studies program and are evaluated in conjunction with the findings reported herein.

METHODS

Readers are referred to earlier reports by Wallace and Romney (1972) and Romney et al. (1973) and those of Beatley (1969, 1974, 1976) for greater details concerning the description of study areas and the results obtained from extensive investigations of soil and vegetation in the northern Mojave Desert areas of the Nevada Test Site. We shall present data in this report from three of

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several different ecotonal transition zones involved in this study.

The first ecotonal study site is located in an open drainage basin (Rock Valley) on the east slope of the Amargosa River watershed. The area sampled is approximately 0.5 km^2 in extent with a downslope length of 500 m. The elevation is about 1050 m, and the slope is to the northwest with a gradient varying from 1 to 3 percent. The dominant and codominant shrub species in this particular ecotonal transition area were separated into three generally homogeneous vegetation zones that were oriented in parallel bands of about the same width, perpendicular to the slope. From 25 to 30 quadrats, 2 × 25 m, were sampled in each zone at coordinate locations generated by a computer program to insure random dispersion. All shrubs were identified by nondestructive dimensional measurements (Romney et al. 1973) from which calculations were made to estimate the spatial distribution. Taxonomy of the area was worked out by Beatley (1969, 1976).

The second ecotonal transect is located across a sharp *Larrea-Atriplex* demarcation line above the playa on the north side of the Frenchman Flat closed drainage basin. Elevation is about 950 m and the slope is to the south at about 2 percent. A 15 × 500 m transect across the ecotonal zone was divided into 50 m sections within which all shrubs were measured.

The third ecotonal transition area studied involved a transect extending down the west-facing bajada onto the Frenchman Lake playa. Five sampling stations were established along the transect, about 1 km apart, at which shrub measurements were made in 2 × 50 m quadrats. Elevation changed from 1040 to 940 m, with the slope varying from 1 to 3 percent at the three sampling sites on the bajada.

Soil sampling pits along each of these transects were dug either by hand or by back-hoe to permit an examination and sampling of the soil profile underneath both shrub and bare areas. The depth of each pit was to the caliche hardpan or, if no restricting layer existed, to a depth well into the C horizon. Profile horizons were described and samples were collected for physical and chemical analysis by the methods of the USDA Salinity Laboratory (1954).

Vegetation samples were collected from each of the sampling sites for subsequent chemical analysis by methods previously described (Romney et al. 1973).

Results and Discussion

Distribution of shrubs within the three vegetation zones investigated in the Rock Valley open drainage basin is listed in Table 1. The zones are numbered 1, 2, and 3, representing upper, intermediate, and lower positions downslope along the transect, respectively.

Edaphic conditions within this ecotonal transition area are typical of the open-drained bajadas we have investigated in southern Nevada. The soil is derived from heterogeneous, highly calcareous alluvium, composed primarily of Cambrian limestones with some tuff and basalt. The surface is a well-developed desert pavement with a massive and strongly cemented caliche layer at depths ranging from 30 to 70 cm. The soil profile horizons are young and often poorly developed. Salt concentrations in the upper profile are relatively low and consist mainly of calcium and magnesium salts. Sodium salts

TABLE 1. Distribution of shrubs in ecotonal zone segments in an open-drainage area of Rock Valley. (Direction of slope →)

	Number of plants per hectare		
Species	Zone 1	Zone 2	Zone 3
Acamptopappus shockleyi Gray	46	0	28
Ambrosia dumosa (Gray) Payne	1844	2474	2504
Atriplex confertifolia (Torr. & Frem.) Wats.	0	0	276
Ephedra nevadensis Wats.	849	845	275
Ceratoides lanata (Pursh) J. T. Howell	155	951	443
Grayia spinosa (Hook) Moq.	203	702	2202
Krameria parvifolia Benth.	1957	951	773
Larrea tridentata (Sesse & Moc. ex DC.) Cov.	1122	907	1004
Lycium andersonii A. Gray	1136	452	83
Lycium pallidum Miers	88	706	815
Total	7400	7988	8403

tend to accumulate at lower depths in the soil profile, especially in local areas where terrain features have restricted drainage. In the case of this particular study area, the main difference in edaphic features was an increase in the silt content of the soil profile, accompanied by an accumulation of sodium salts at depths below 30 cm, proceeding downslope along the transect.

Each of the shrub species present in this transition zone exhibit some degree of facultative adaptation for salt tolerance, but none is known to have obligate requirements (Wallace and Romney 1972, Wallace et al. 1973a, 1973b, 1974). Those species which increase in density in zones progressing downslope are the ones that commonly are more salt tolerant in nature. Notably so are *Ambrosia dumosa* (A. Gray) Payne, *Atriplex confertifolia* (Torr. & Frem.) Wats., *Grayia spinosa* (Hook) Moq., and *Lycium pallidum* Miers. There also was an interaction with soil texture in this area. *Ambrosia dumosa*, *Ceratoides lanata* (Pursh) J. T. Howell, and *L. pallidum* are better adapted to finer textured soils than *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. or *Lycium andersonii* A. Gray, and these species responded accordingly at this study site.

The second transect is across a sharp ecotonal demarcation line between *L. tridentata* and *Atriplex canescens* (Pursh.) Nutt. communities situated between the bajada and playa of the Frenchman Flat closed drainage basin. Plant distribution along the transect is shown in Table 2. The analyses disclosed an ecotonal demarcation zone among several other species at this study site that is not so apparent from visual observations. The transition across the ecotone was equally sharp among several plant species. The distribution patterns for *A. dumosa*, *C. lanata* and *L. tridentata* were much more alike than under the situation given in Table 1. Different edaphic factors, therefore, could be involved. Since *C. lanata* distribution paralleled *L. tridentata*, one might conclude that soil salinity is not a simple causal factor at this particular ecotone, inasmuch as *C. lanata* can grow in moderately saline soil (Vest 1962) but *L. tridentata* does not. An alternative explanation could be that ecotypes are differentially sensitive to salt. We hasten to point out, therefore, that the distribution of *C. lanata* extended well beyond the *Larrea* demarcation line onto the playa at some of the other transects investigated elsewhere around the ecotone.

It should be taken into account that sensitivity of seeds and young seedlings to soil salinity and to pH could be limiting causal factors at this ecotone, either at the present time or earlier when the population initially became established. The soil profiles along this transect showed surface pH values ranging from 8.0 to 9.0. The soluble salts at the surface were moderate (EC_{25} varied from 2.07 to 3.06 mmhos/cm). Salt accumulations, including soluble boron and nitrate, generally increased at greater depths in the soil profile within the playa. In some earlier work, Barbour (1968) observed that *L. tridentata* seed germination was not affected by high soil pH but that subsequent seedling development was markedly decreased, especially above pH 8.0. The lack of any young seedlings in the ecotonal area suggests that seedling survival is a rare event that may be partially regulated by the high soil pH levels now present. Size stratification occurs within the shrub population, however, which indicates that favorable moisture conditions for seedling sur-

TABLE 2. Distribution of plant species along a 500 m transect across the *Larrea-Atriplex* ecotone line in north Frenchman Flat. (Direction of slope →)

Species	Number of plants in 15 × 50 m segments									
Ambrosia dumosa (Gray) Payne	263	168	96	16	47	29	23	14	0	0
Atriplex canescens (Pursh.) Nutt.	54	47	74	100	149	246	183	192	240	202
Ceratoides lanata (Pursh) J. T. Howell	99	84	52	10	25	6	4	2	1	1
Larrea tridentata (Sesse & Moc. ex DC.) Cov.	55	75	40	54	28	3	0	1	0	0
Lycium andersonii A. Gray	2	5	3	1	0	0	1	0	0	0
Salsola iberica Sennen & Pau	1	0	0	0	18	54	42	56	44	56
Sphaeralcea ambigua Gray	37	61	50	106	49	121	126	129	256	203

vival have occurred periodically, presumably many decades apart.

Another factor thought to be involved in regulating shrub distribution at this ecotone is periodic flooding of the basin floor beyond the boundaries of the dry lake bed. Shrubs that are sensitive to poor root aeration or standing water on foliage can be damaged when inundated with flood water. A case in point was observed recently near Baker, California (Wallace and Romney 1972). *Larrea tridentata* is known to require good aeration of the root zone and well-drained soils (Shreve and Wiggins 1964). Complete inundation need not be effected to keep *L. tridentata* from populating a site; a higher than normal water table could be just as detrimental to some sensitive species.

Monitoring of soil and air temperatures from May 1967 to January 1973 gave very little indication that a temperature differential across this ecotone was an important causal factor compared to the edaphic features.

The mineral element composition of shrubs did not differ significantly across the ecotonal transition zone. Data in Table 3 for shrubs sampled near the middle of the transect are representative of those sampled elsewhere along the ecotone. The uniformity of mineral composition (i.e., cation and anion balance) in these salt-tolerant shrubs, irrespective of location and edaphic conditions (Romney et al. 1973), attests to their adaptive capacity to regulate their own salt balance.

The distribution of shrub species along the 5 km ecotonal transect across the bajada and playa in east Frenchman Flat is shown in Table 4. Species diversity became less complex progressing downslope onto the bajada. These data are a good example of how the more sensitive species give way to the more salt-tolerant ones under changing edaphic conditions. It would not be prudent in this instance, however, to assume that increasing salinity was the only causal factor of community or species distribution. Factors of moisture stress and soil texture also must be taken

TABLE 3. Mineral composition of leaves of shrubs from the north Frenchman Flat ecotonal zone.

Species	N	Cl	S	P	Na	K	Ca	Mg	B
				Percent of dry weight					ug/g
A. dumosa	3.68	0.85	0.71	0.44	0.08	5.63	2.28	0.53	130
A. canescens	2.44	1.65	1.80	0.15	1.05	8.02	3.80	1.14	60
C. lanata	2.79	0.41	0.34	0.19	0.10	3.38	1.67	0.43	49
L. tridentata	2.37	0.68	0.12	0.29	0.03	2.53	1.64	0.19	76
L. andersonii	2.32	1.00	0.85	0.24	0.03	6.30	9.92	0.91	75
S. ambigua	2.12	0.31	0.26	0.72	0.13	3.35	2.98	0.53	160

TABLE 4. Shrub distribution across a 5 km ecotonal transect in east Frenchman Flat. (Increasing salt gradient →)

Species	Percent frequency at sampling sites*				
	1	2	3	4	5
Acamptopappus shockleyi Gray	2.1	9.2	—	—	—
Ambrosia dumosa (Gray) Payne	2.4	59.2	13.5	—	—
Atriplex canescens (Pursh) Nutt.	—	—	5.0	90.2	—
Atriplex confertifolia (Torr. & Frem.) Wats.	6.4	—	43.2	9.8	100
Psorothamnus fremontii (Torr.) Barneby	19.1	—	—	—	—
Ephedra nevadensis Wats.	4.3	—	—	—	—
Ceratoides lanata (Pursh) J.T. Howell	6.5	6.6	5.4	—	—
Hymenoclea salsola T & G.	4.3	—	5.4	—	—
Krameria parvifolia Benth.	8.5	1.3	—	—	—
Larrea tridentata Ses	40.4	13.2	24.3	—	—
Sphaeralcea ambigua Gray	2.1	—	2.7	—	—
Thamnosma montana Torr. & Frem.	2.1	—	—	—	—
Yucca brevifolia Engelm. in Wats.	2.1	6.6	—	—	—

*Shrubs contributing less than 1 percent are unlisted.

into account because marked changes occurred, progressing downslope onto the playa.

Some soil properties at the different sampling sites across the East Frenchman Flat transect are listed in Table 5. Increased soil salinity occurred, especially at the two sites along the playa where only the two *Atriplex* species grew in abundance. Calcium dominated the soluble cation pattern in the upland area of the transect, and sodium became more dominant on the playa, as one might expect in a closed drainage basin. Chloride and nitrate concentrations increased in the soil profile of the dry lake playa.

The east Frenchman Flat transect is a good example relating salinity to community or species distribution. On the other hand, this relationship was not so clear-cut at several other transects across the ecotonal zone, surrounding the Frenchman Dry Lake playa (Romney et al. 1973), where better correlation occurred with the edaphic features of soil moisture stress and texture. This has been the experience of other investigators where attempts to relate salinity alone to community or species distribution gave inconsistent results (Gates et al. 1956, Branson et al. 1967). Branson et al. (1970) speculate that upland halophytes dominate certain areas because of tolerance to high osmotic stress or high physical moisture stress, or a combination of both. We find indications of this occurring at our study areas in southern Nevada. We also see much evidence, as expressed by Unger (1966), "that the most salt-tolerant species have the widest salinity tolerance and can survive under low as well as high salinities. The less tolerant species are limited in their distribution to low and nonsaline areas."

A summary of the bibliography of the vegetation and soils of Nevada was compiled by Tueller et al. (1971).

Acknowledgment

This study was supported by Contract EY-76-C-03-0012 between the U.S. Department of Energy and the University of California.

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TABLE 5. Soil properties (30 cm depth) across the 5 km transect in east Frenchman Flat. (Direction of slope →)

Soil properties	Site 1	Site 2	Site 3	Site 4	Site 5
pH, sat. extract	8.7	8.7	8.8	8.8	8.9
EC_{25}, mmhos/cm	2.15	1.89	1.00	2.40	2.98
Saturation extract ions					
Na (meq./liter)	3.57	1.37	2.47	15.45	27.95
K (meq./liter)	6.13	4.48	2.48	5.25	3.98
Ca (meq./liter)	22.69	17.39	6.93	11.78	6.79
Mg (meq./liter)	8.97	5.85	3.65	12.43	4.80
Cl (meq./liter)	1.26	1.40	2.28	6.37	12.66
NO_3 (meq./liter)	6.62	6.16	5.00	17.50	23.10
SO_4 (meq./liter)	0.52	0.41	0.40	0.54	0.59
Exch. Na, percent	2.0	2.2	2.9	6.2	22.1

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